PARASITISM OF GREATER PRAIRIE-CHICKEN NESTS BY RING-NECKED PHEASANTS

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Abstract: We studied nest parasitism of greater prairie-chickens (*Tympanuchus cupido pinnatus*) by ring-necked pheasants (*Phasianus colchicus*) as a possible contributing factor in the decline of an isolated population of prairie-chickens in Jasper County, Illinois. Both species nested in small, scattered grasslands maintained on prairie-chicken sanctuaries. Incidence of parasitic laying by pheasant hens in prairie-chicken nests increased from 2 to 43% between 1970 and 1983 and remained high through 1987. Nest success ($\geq$1 host-egg hatching) did not differ (P = 0.33) between 60 unmanaged parasitized nests (43%) and 602 unparasitized nests (51%). However, success of 14 parasitized prairie-chicken nests managed by removal of pheasant eggs (86%) was greater (P = 0.02) than for 24 unmanaged parasitized nests (46%) during 1983 and 1985–87. Hatchability of fertile prairie-chicken eggs was less (P < 0.01) in parasitized nests (77%, conservatively) than in unparasitized nests (94%), because of earlier hatching of pheasant eggs, increased embryo mortality of prairie-chickens, or increased nest abandonment. Large clutches of prairie-chicken eggs typical of early nests were more likely (P < 0.001) parasitized than small clutches laid later. Factors correlated with rate of nest parasitism included numbers of pheasant cocks (P = 0.01) and numbers of pheasant nests (P < 0.001) found each year. Although pheasant control apparently eliminated nest parasitism during 1988–94, prairie-chicken numbers continued to decline. Without management intervention to control pheasants on sanctuaries, the survival of this isolated, remnant flock of prairie-chickens may be in greater jeopardy.

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Interspecific parasitism of nests by female ring-necked pheasants (hereafter, pheasant) is relatively common (Finley 1896; Tegetmeier 1904:14–17; Bennett 1936, Kimmel 1988). Although pheasants have been established for over a century in North America, few data exist regarding the effects on host species of their proclivity to parasitize nests of native birds. The difference in incubation periods between greater prairie-chicken (hereafter, prairie-chicken) and pheasant eggs also presents a potential problem for the host species. Prairie-chicken eggs require about 25 days of incubation (McEwen et al. 1969, Svedarsky 1979), whereas pheasant eggs require about 23 days (Dale 1956, Labisky and Opsahl 1958). Prairie-chicken hens cease incubation, begin brooding, and depart from their nests within 24 hr after the first egg hatches (Gross 1930, Schwartz 1945). Thus, if pheasants parasitize prairie-chicken nests prior to incubation, pheasant eggs may hatch first and prairie-chicken hens may leave their nests with pheasant chicks and few, if any, of their own offspring (Vance and Westemeier 1979). Variation in nest success and brood survival are thought to be important determinants of prairie-chicken population dynamics (Hamerstrom et al. 1957, Kirsch 1974, Wisdom and Mills 1997).

Pheasants were introduced in Illinois shortly before 1900, and rapid increases in distribution and abundance occurred from the 1920s to 1942 (Robertson 1958). Pheasants were not considered a factor in the decline of prairie-chickens in southern Illinois prior to establishment of pheasants in Jasper County (Yeatter 1943, 1963). Pheasants were few and interactions with prairie-chickens were not evident during the early development (1962–69) of sanctuaries for prairie-chickens in Jasper and Marion counties (Westemeier 1973). By 1970, however, pheasants occasionally were observed in aggressive interactions with prairie-chicken cocks on booming grounds and were parasitizing prairie-chicken nests (Vance and Weste-

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meier 1979). By 1981, pheasant densities on sanctuaries in Jasper County (8 cocks/km^2) were about 40 times the density of pheasants on adjacent private land (Westemeier 1984). By spring 1993, only 2 flocks totaling about 50 prairie-chickens were found on or near 2 clusters of grassland sanctuaries. Translocations of prairie-chickens from Minnesota, Kansas, and Nebraska began in August 1992 to enhance the genetic and demographic potential of the remaining prairie-chickens in Illinois (Westemeier and Jansen 1995).

Our purpose is to describe trends in rates and effects of parasitism by pheasants on prairie-chicken nests before, during, and after efforts to reduce pheasant abundance on prairie-chicken sanctuaries in Illinois. Specifically, we related indices of pheasant and prairie-chicken abundance to rates of nest parasitism and compared nest success, clutch size, fertile eggs per clutch, egg fertility, egg success, hatchability of fertile eggs, and embryo mortality between parasitized and unparasitized prairie-chicken nests.

STUDY AREA

The primary study area near Bogota, Jasper County, Illinois, consisted of private farmland and 9 managed grassland tracts (sanctuaries) in 9 adjoining sections of land (Fig. 1) on the southern edge of the contiguous range of pheasants (Warner 1981). Sanctuaries ranged in size from 7 to 94 ha (total = 486 ha) and typically were subdivided into fields averaging 4 ha (Westemeier 1973, Westemeier and Buhnerkempe 1983, Buhnerkempe et al. 1984; Westemeier 1984, 1988). Sanctuaries were islands of breeding habitat for grassland birds in a matrix of soybeans, corn, and wheat, with limited nesting and brood-rearing habitat.

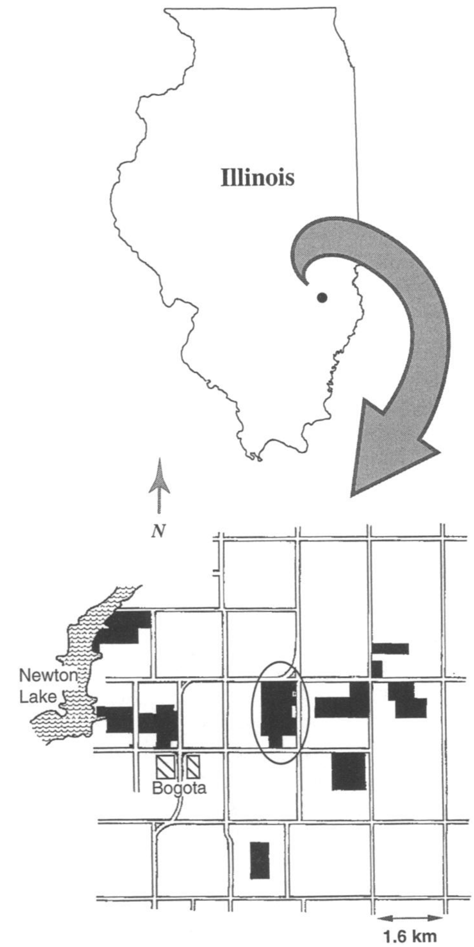

Fig. 1. Greater prairie-chicken sanctuaries (black blocks) studied in Jasper County, Illinois, to determine effects of parasitism by ring-necked pheasants on greater prairie-chicken nests. During 1963–94, 58% of 965 greater prairie-chicken nests examined and 69% of 74 cases of parasitism were observed on the 94-ha Yeatter-Field-McGraw (YFM) Sanctuary (circled). Parasitism of greater prairie-chicken nests on the YFM was 60% during 1985–87.

METHODS

Population Monitoring and Pheasant Control

Booming ground surveys followed methods described by Hamerstrom and Hamerstrom (1973) and were conducted on an 83-km^2 block encompassing the sanctuaries (Westemeier 1988). We used 32 1-min listening stops spaced at 1.6-km intervals during the peak of hen visitation from late March through early April (1963–97) to locate all booming grounds. Male and female prairie-chickens were counted separately on each booming ground on at least 3 mornings. Although pheasants were counted when prairie-chickens were counted, the same route was repeated during late April and early May, with 4-min stops to record pheasants during the peak of crowing. Volunteer observers aided census efforts by recording counts and other observations from blinds on booming grounds. Pheasant control was limited to sanctuaries and consisted of occasional opportunistic shooting from 1975 through 1984 (Vance and Westemeier 1979). Intensive control efforts during 1986–87 involved teams of experienced wing shooters, use of artificial nests, intensive nest searching to collect pheasant eggs and hens, and limited trapping (Westemeier 1988).

Since 1988, pheasant numbers were maintained at low levels by habitat manipulations to concentrate pheasants for shooting principally when snow facilitated tracking.

Nest Searches and Assessment

During 1963–87, all potential nest cover was intensively searched once annually on 142 ha of 2 sanctuaries in Jasper County (the Yeatter-Field-McGraw [YFM] unit plus the Donnelley unit to the east; Westemeier 1988). Data from partial searches of nest cover on other nearby sanctuaries also were included in annual datasets. Nests were located by walking and visually inspecting growing and residual vegetation with a 1.5-m staff (Westemeier and Buhnerkempe 1983, Buhnerkempe et al. 1984). In 1993–94, nests initiated by translocated radiomarked prairie-chickens were examined for pheasant eggs; however, these nests were not included in density estimates, because we did not search for nests of unmarked hens.

During 1963–84, nest searches were made after the hatch peak of about 1 June, by which time >95% of nest initiations by prairie-chickens would have occurred (Yeatter 1943; R. L. Westemeier, unpublished data). During 1985–91, searches began about 1 May to facilitate removal of pheasant eggs from active prairie-chicken nests.

We used apparent nest success to compare parasitized and unparasitized prairie-chicken nests because 88% of nests were hatched, depredated, or abandoned when discovered. We considered parasitized and unparasitized nests successful for prairie-chickens if ≥1 prairie-chicken egg hatched; thus, we included parasitized nests in which both prairie-chickens and pheasants hatched. Nests in which only pheasants hatched were considered as abandoned. Abandonment by prairie-chickens may have been underestimated because some abandoned nests may have been destroyed by predators before they were examined.

To determine egg success for parasitized nests, we included prairie-chicken eggs that were incubated long enough to hatch pheasants (≥23 days). To assess mortality and estimate age at death, dead embryos were excised from intact eggs of prairie-chickens and pheasants and aged using a guide by Labisky and Opsahl (1958). Sample sizes for determining incubated clutch size, egg fertility, egg success (hatched eggs/total eggs), hatchability (hatched eggs/fertile eggs), and embryo mortality (dead embryos/incubated fertile eggs) depended on the condition of egg contents and shell remains when nests were discovered. We emphasized hatchability because egg fertility needed to be considered as a possible bias in comparing parasitized and unparasitized clutches.

Data Analyses

We hypothesized that rates of nest parasitism would correlate with numbers or densities of pheasant cocks, with prairie-chicken cocks, or with numbers or densities of nests of each species. To determine which variables had the strongest associations, we calculated Pearson's correlation coefficients (Zar 1984) between the numbers of parasitized nests or rates of parasitism each year and the following: (1) numbers of pheasant cocks within the 83-km^2 census area, (2) numbers of pheasant cocks on or within 0.4 km of sanctuaries, (3) numbers of pheasant cocks per square kilometer of sanctuary grassland, (4) numbers and densities of pheasant nests (yearly totals and nests/10 ha of searched grassland), and (5) numbers and densities of prairie-chicken cocks and nests on or within 0.8 km of sanctuaries. Distances of 0.4 and 0.8 km were chosen subjectively to include pheasant cocks observed (or heard) near sanctuaries and prairie-chickens using booming grounds adjacent to sanctuaries. Percentage data were arcsine transformed. For calculating correlations, we used data from 1969 to 1987 because the area searched ($\bar{x}$ = 156 ± 6.1 ha) for nests was relatively consistent during those 19 years. The area searched was smaller and varied during the years 1988–91 ($\bar{x}$ = 80 ± 20.9 ha); moreover, intensive pheasant control potentially confounded results during the latter period.

Because data on nest success were not normally distributed, we used nonparametric statistics to test the following hypotheses: (1) success, depredation, and abandonment of prairie-chicken nests were independent of parasitism by pheasants; and (2) nests with ≤3 parasitic pheasant eggs were no more successful than nests with >3 parasitic pheasant eggs. First, we used Fisher's exact tests (1 df for all; Mehta and Patel 1995) to assess differences in nest success between managed (pheasant eggs removed prior to hatching) and unmanaged (pheasant eggs not removed) parasitized nests. When differences existed, we deleted managed nests from

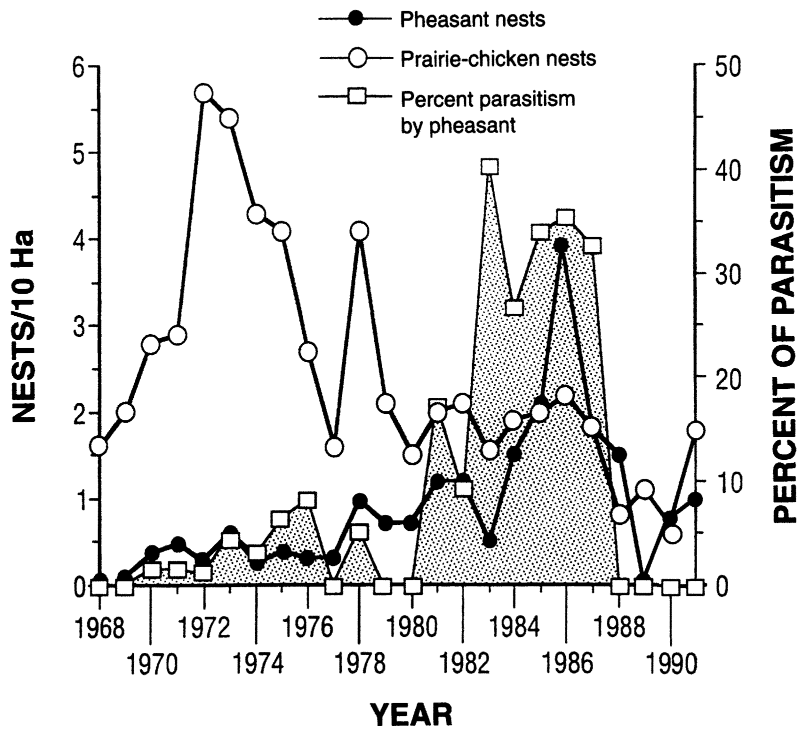

Fig. 2. Nest densities (nests/10 ha of searched grassland) for ring-necked pheasants and greater prairie-chickens, and percent parasitism (shaded) of greater prairie-chicken nests by ring-necked pheasants on the Bogota study area, Jasper County, Illinois, 1968–91.

the sample and ran separate analyses to compare unmanaged parasitized nests with unparasitized nests. We then used Fisher's exact test to compare rates of depredation and abandonment.

To evaluate differences between parasitized and unparasitized nests in clutch size, egg fertility, egg success, hatchability of fertile eggs, and embryo mortality, we used a normal approximation to the Mann-Whitney test with Z-values for continuous distributions and critical values for the t-distribution (Zar 1984). We also used Mann-Whitney exact tests (Mehta and Patel 1995) to assess differences in egg success, hatchability of fertile eggs, and embryo mortality between managed and unmanaged clutches. Removal of pheasant eggs from parasitized prairie-chicken nests by investigators did not bias clutch size or egg fertility, because our interventions occurred after these parameters were determined. We used the Kolmogorov-Smirnov (K-S) goodness-of-fit test for ordinal data (Zar 1984; d_{max} test statistic) to determine if embryo mortality of prairie-chickens was uniformly distributed among 5-day age classes during embryo development of unparasitized (undisturbed, disturbed) and parasitized (unmanaged, managed) nests. For all tests, significance was assumed when $P < 0.05$. All means are reported $\pm$ standard error.

RESULTS

Incidence of Nest Parasitism

In Jasper County during 1963–94, we examined 965 prairie-chicken nests of which 112 (12%) were active (laying or incubation underway) when located; 929 nests were on 8 of the 9 sanctuaries, and 36 were on nearby private land. The YFM Sanctuary accounted for 561 (58%) of total nests and 51 of 74 (69%) parasitized nests. Nest parasitism by pheasants was not observed among 115 prairie-chicken nests located during 1963–69. The first pheasant nest on a sanctuary was found in 1969, and the first documented parasitism of a prairie-chicken nest in Illinois was recorded at Bogota in 1970 (Vance and Westemeier 1979). Mean rates of nest parasitism remained low (3.1 $\pm$ 0.9%) or parasitism was not detected during 1969–80, when the mean density of pheasant nests was low (0.5 $\pm$ 0.07/10 ha of searched grassland;

Table 1. Fate of greater prairie-chicken nests relative to the number of parasitic eggs deposited by ring-necked pheasants, Jasper County, Illinois, 1970–87.

Pheasant eggs/ prairie-chicken nest	Nests with ≥1 hatched pheasant egg		Fate: Successful[a]		Depredated		Abandoned		Total
	n	%	*n*	%	*n*	%	*n*	%	*n*
0	0		307	51.0	255	42.4	40	6.6	602
1–3	20	44.4	23	51.1[b]	19	42.2	3	6.7	45
4–11	7	46.7	3	20.0[b]	6	40.0	6	40.0	15
Totals	27	45.0	333	50.3	280	42.3	49	7.4	662

[a] ≥1 prairie-chicken hatched.
[b] Success of parasitized nests (43.3%) did not differ (P = 0.28) from unparasitized nests. However, 21 of 26 parasitized nests that were successful for prairie-chickens also hatched pheasants, resulting in mixed broods with unknown consequences for prairie-chicken chicks.

Fig. 2). Mean densities of pheasant cocks on or within 0.4 km of sanctuaries also were low (5.0 ± 0.6/km^2 of sanctuary grassland) during that period, and during 1988–94 (3.0 ± 0.4/km^2), when control measures were applied.

Densities of prairie-chicken nests peaked in 1972 (5.9/10 ha) and then gradually declined as nest parasitism and densities of pheasant nests increased (Fig. 2). During 1981–87, mean densities of pheasant cocks (10.0 ± 2.0/km^2) and pheasant nests (1.9 ± 0.4/10 ha) were highest, and 54 of 188 (29%) prairie-chicken nests were parasitized (range = 9–43% annually). On the 94-ha YFM Sanctuary, which consistently contained the largest numbers of prairie-chickens and their nests, parasitism was 60% during 1985–87. In contrast, after intensive pheasant control was initiated in 1986 (Westemeier 1988), no parasitism occurred among 47 prairie-chicken nests during 1988–94. Despite the absence of parasitism after 1987, however, prairie-chicken numbers at Bogota (205 cocks in 1973) continued a downward trend that began in 1973. Only 6 cocks from this Illinois population remained in 1994. Translocations of prairie-chickens from Minnesota, Kansas, and Nebraska began in August 1992; by spring 1996, 70 cocks were counted at Bogota (Westemeier and Jansen 1995, Westemeier 1997).

Positive linear correlations (n = 19, 17 df for all correlations) were detected between numbers of prairie-chicken nests parasitized each year and numbers of pheasant cocks within the 83-km^2 census area (r = 0.71, P = 0.01), and between numbers of prairie-chicken nests parasitized and numbers of pheasant nests found on sanctuary grasslands (r = 0.79, P < 0.001). Negative correlations were detected between numbers of prairie-chicken cocks and the proportion of prairie-chicken nests parasitized the previous year (r = −0.59, P < 0.01), and between numbers of prairie-chicken nests found and the proportion of prairie-chicken nests parasitized the previous year (r = −0.57, P < 0.02). Correlation values were the same (r = 0.71), lower (r = 0.60 or −0.51), or not significant (r = −0.41) when densities of cocks and nests were used instead of abundance in the preceding calculations.

Success of Parasitized Prairie-Chicken Nests

During 4 years (1983, 1985–87), success of parasitized nests managed by removal of pheasant eggs (86%; n = 14) was greater (Fisher's exact test = 5.86, P = 0.02) than for unmanaged parasitized nests (46%; n = 24). When managed nests were excluded, success of parasitized (43%) and unparasitized (51%) nests did not differ (Fisher's exact test = 1.28, P = 0.28; Table 1). However, the 26 unmanaged successful nests included 21 that hatched both prairie-chickens and pheasants and resulted in mixed broods. Five unmanaged parasitized nests incubated sufficiently to hatch pheasants were not considered successful, because prairie-chicken eggs with developing embryos were abandoned. Unmanaged parasitized prairie-chicken nests with 1–3 parasitic pheasant eggs were more successful (51%; Fisher's exact test: 4.39, P = 0.04) than unmanaged parasitized nests with 4–11 parasitic eggs (20%; Table 1).

Nest losses due to predation were similar (Fisher's exact test: 0.02, P = 1.00) between unparasitized and unmanaged parasitized clutches (Table 1). However, minimum rates of abandonment differed between unparasitized (7%) and unmanaged parasitized (15%) nests (Fisher's exact test: 5.04, P = 0.03).

Prairie-Chicken Eggs in Parasitized Nests

Mean clutch size of host eggs in incubated prairie-chicken nests was greater (P < 0.001)

Table 2. Reproductive outcome of eggs from unparasitized greater prairie chicken nests compared with host eggs from greater prairie-chicken nests parasitized by ring-necked pheasants, Jasper County, Illinois, 1970–87. Data include only nests for which the number of eggs was the total laid in each nest and include only years with data for unparasitized and parasitized nests.

Reproduction parameter	Unparasitized			Parasitized				
	Mean	SD	*n*	Mean	SD	*n*	Z^a	*P*
Clutch size	11.5	2.4	122	13.4	2.0	35	4.35	<0.001
Fertile eggs/clutch	10.9	2.9	80	12.4	2.1	23	2.30	<0.025
Egg fertility (%)	94.0	10.4	74	90.5	10.5	23	1.55	0.066
Egg success[b] (%)	85.9	17.7	112	63.0	35.3	30	3.16	<0.001
Hatchability[c] (%)	94.0	14.9	77	77.2	31.2	23	2.96	<0.003
Embryo mortality[d] (%)	6.4	14.9	77	21.6	31.5	23	2.62	<0.005

[a] Normal approximation to the Mann-Whitney *u*-test for differences between parasitized and unparasitized nests.
[b] Hatched eggs/total eggs.
[c] Hatched eggs/fertile eggs.
[d] Dead embryos/incubated fertile eggs.

among parasitized versus unparasitized nests (Table 2). As expected, the mean number of fertile prairie-chicken eggs in parasitized clutches also was larger than in unparasitized clutches. However, percent fertility was similar for prairie-chicken eggs in unparasitized and parasitized nests. Further, clutch size of prairie-chicken eggs was not correlated (r_{33} = 0.16, P = 0.37) with numbers of pheasant eggs in parasitized clutches.

To evaluate overall egg success and hatchability of fertile eggs, managed and unmanaged parasitized nests were combined to compare with unparasitized nests because no differences could be attributed to management (egg success: U = 45.5, P = 0.79; hatchability: U = 32.0, P = 0.94). Sufficient data then were available to determine egg success for 30 prairie-chicken nests (Table 2). These data included eggs from 26 nests in which 2–14 prairie-chickens hatched, and 4 nests in which only pheasants hatched. Percent success of host eggs was lower (P < 0.001) in parasitized nests than in unparasitized nests (Table 2). Similarly, percent hatchability of fertile host eggs also was lower (P < 0.003) in parasitized nests than in unparasitized nests.

Embryo Mortality

The ratio of dead embryos to incubated fertile eggs did not differ (U = 39.0, P = 0.71) between successful prairie-chicken nests from which parasitic pheasant eggs had been removed (16%; n = 12) and those from which pheasant eggs were not removed (17%; n = 12). Thus, managed and unmanaged parasitized nests again were combined. When data were used from successful clutches in which embryos from unhatched eggs could be clearly identified, embryo mortality in 23 parasitized nests was 3.4 times that in 77 unparasitized nests (P < 0.01; Table 2).

Timing of Embryo Mortality

Mortality was not uniformly distributed (K-S = 10.2, P < 0.001) among age classes for 151 dead prairie-chicken embryos suitable for aging (Table 3). Most (66%) embryos died within 5

Table 3. Percentage of dead greater prairie-chicken embryos in successful nests (≥1 greater prairie-chicken or ring-necked pheasant hatched), by age class and nest category, Jasper County, Illinois, 1975–87.

Nest category	Nests (*n*)	Dead embryos (*n*)	Age class (days)					P^a
			0–4.9	5–9.9	10–14.9	15–19.9	20–24.9	
Unparasitized	17	49	16.3	24.5	16.3	2.0	40.8	<0.020
Undisturbed	9	25	12.0	24.0	8.0	0.0	56.0	<0.002
Disturbed[b]	8	24	20.8	25.0	25.0	4.2	25.0	>0.500
Parasitized	18	102	9.8	7.8	2.9	1.0	78.4	<0.001
Unmanaged	12	79	1.2	2.5	2.5	1.2	92.4	<0.001
Managed[c]	6	23	39.1	26.1	4.3	0.0	30.4	>0.050
Totals	35	151	11.9	13.2	7.3	1.3	66.2	<0.001

[a] Kolmogorov-Smirnov goodness-of-fit test for discrete ordinal scale data. Distribution among age classes is not uniform when P < 0.05.
[b] Disturbed = incubating hen flushed by investigators.
[c] Managed = pheasant eggs removed by investigators prior to hatching.

days of expected hatching time, especially in parasitized nests from which pheasant eggs had not been removed (K-S = 59.6, $P < 0.001$). No departures from a uniform distribution of embryo mortality were detected among unparasitized nests from which hens were flushed to check for pheasant eggs (K-S = 2.6, $P > 0.50$), or among nests where pheasant eggs were removed (K-S = 5.8, $P > 0.50$). Most (62–65%) of the 47 dead embryos found in disturbed nests died before we flushed incubating hens, suggesting causative factors other than investigator disturbance.

We found 1 clutch containing the shell of a hatched pheasant egg and 13 unhatched prairie-chicken eggs, 10 of which had pipped. There were ≥4 instances in which parasitized clutches of 12–13 prairie-chicken eggs with full-term embryos were abandoned, apparently because host hens left their nests with pheasant chicks that had already hatched.

DISCUSSION

Incidence of Nest Parasitism

After 7 years with no observed nest parasitism at Bogota, the incidence of parasitism increased gradually during 1970–87 and peaked at 43% in 1983. In 3 of these years, 60% of nests were parasitized in the core of the study area. No parasitism was observed during 7 years (1988–94) when pheasants were controlled, but prairie-chicken numbers continued the decline that began in 1973. Rates of parasitism probably would have reached higher levels without the pheasant control initiated in 1986 (Westemeier 1988). Parasitism of prairie-chicken nests was positively correlated with numbers of pheasant cocks and nests; correlations between rates of nest parasitism and numbers of prairie-chicken cocks and nests counted during the following spring were negative. From 32 to 62% (r^2 values) of the variation in nest parasitism was associated with measures of pheasant abundance.

The incidence of parasitism by pheasants on prairie-chicken nests probably reflects the dependence of both species on limited nesting habitat (Westemeier 1973, Vance and Westemeier 1979, Westemeier 1988), and the tendency of pheasants to drop eggs, dump nest (Buss et al. 1951, Stokes 1954), and parasitize nests of an array of ground-nesting birds (Kimmel 1988). The generality of our results is difficult to assess; however, aggressive interactions between these species were reported in the Nebraska Sandhills (Sharp 1957) and in southern Wisconsin, northern Illinois, and northern Indiana (Cahalane et al. 1942, Westemeier and Edwards 1987). Despite large overlaps of range, we know of only 1 other instance of pheasants parasitizing prairie-chicken clutches: Carlson (1942) reported single pheasant eggs in 2 prairie-chicken nests in Minnesota.

Nest parasitism by pheasants may be minimal whenever pheasant densities are low. On Illinois sanctuaries during the 12 years 1969–80, for example, the average rate of nest parasitism was low (3%) when densities of pheasants averaged 5 cocks/km^2 of sanctuary grassland, and densities of pheasant nests averaged 0.5/10 ha (Fig. 2). Such levels of pheasant abundance may be the maximum allowable for management of Illinois prairie-chicken sanctuaries. In contrast, parasitism averaged 29% during 1981–87 when pheasant densities on or near sanctuary grasslands averaged 10 cocks/km^2 and 1.9 nests/10 ha.

Reduced Productivity Resulting From Parasitism

The high success (86%) among 14 prairie-chicken nests from which pheasants eggs were removed prior to hatching suggests more of the 60 unmanaged nests would have been successful had they not been parasitized. Such intensive management is impractical on a large scale and was not effective for decreasing embryo mortality. Thus, success of parasitized nests, defined as ≥1 host egg hatching, may have limited relevance to sustaining a wild population if hatchability of fertile eggs in parasitized clutches is less than in unparasitized nests. Among the 43 nests in which ≥1 prairie-chicken or pheasant hatched, parasitism reduced hatchability and egg success by 18–27%. These were conservative "best-case" estimates because calculations excluded nests with uncertain numbers of eggs and those containing eggs with contents too decomposed to reliably assess fertility. For example, hatchability may have been <77% (Table 2) because numbers of fertile prairie-chicken eggs could not be determined for 4 nests that hatched pheasants but not prairie-chickens. Further, removal of pheasant eggs from some parasitized nests prior to hatching (Westemeier 1988) may have confounded estimates of hatchability, particularly in 1986–87.

To derive a "worst-case" estimate of hatchability of host eggs in parasitized nests, we used the average fertility rate of 0.94 from unparasitized nests (Table 2) and data on clutch size and numbers of hatched eggs from unmanaged nests during 1981, 1984, and 1985, when pheasants were relatively numerous. In 14 parasitized clutches with 184 eggs, 83 eggs hatched from 173 fertile host eggs, yielding a hatchability rate of 0.48. Multiplying the 43 parasitized nests that hatched prairie-chickens or pheasants times 12.4 (173/14) fertile host eggs/clutch yields 533 prairie-chicken embryos. In contrast, production would be 256 prairie-chicken chicks if true hatchability was 48%, a reduction of 49% from the "norm" (94%), due to nest parasitism. Even with 77.2% hatchability (rather than 94%) of 12.4 fertile eggs/parasitized clutch (Table 2), the result is 1.85 less chicks/brood at hatching. Peterson and Silvy (1996) reported 1.78 less chicks/brood among Attwater's prairie-chickens (*T. c. attwateri*) than among greater prairie-chickens, and they concluded the difference was important for recruitment.

A major limitation of our study is the unknown survival of host chicks hatched with pheasants. Of 31 unmanaged parasitized nests in which prairie-chickens or pheasants hatched, only 5 (16%) resulted in prairie-chicken chicks leaving nests unencumbered by parasitic brood mates. Survival of prairie-chicken chicks with or without parasitic brood mates should not be assumed equal, because pheasant chicks are larger and more aggressive than prairie-chicken chicks. In captivity, for example, McEwen et al. (1969:278) observed that pheasant chicks "peck and harass the smaller grouse chicks." Efforts (R. L. Westemeier, unpublished data) to use 1 pheasant chick to "train" 4 young prairie-chickens to eat commercial feed were thwarted by the pheasant's repeated pecking of grouse chicks. Although anecdotal, these observations suggest survival may decrease among young prairie-chickens accompanied by pheasant chicks. Moreover, the 4 prairie-chicken hens that hatched only pheasants from parasitized clutches indicate prairie-chicken hens respond to stimuli from newly hatched pheasant chicks. These observations suggest prairie-chicken hens may abandon clutches or begin brooding foster chicks when pheasants hatch.

Ultimate Effects of Nest Parasitism

Success during nesting and brood rearing is vital for prairie-chicken populations (Wisdom and Mills 1997). Results from our study suggest mechanisms whereby interspecific nest parasitism may reduce recruitment and abundance of prairie-chickens. However, because prairie-chickens did not increase after pheasant control eliminated nest parasitism, factors other than parasitism also must have been operating. Other factors include regional habitat loss and isolation of remnant prairie-chicken populations in Illinois, accompanied by declines in numbers, fitness, and genetic diversity (Westemeier et al. 1991, Westemeier and Jansen 1995, Bouzat et al. 1998).

Extirpations of prairie-chickens attributed to interactions with pheasants have been reported in Wisconsin, Illinois, and Indiana (Cahalane et al. 1942), and in central Michigan (W. N. Bronner and G. D. Stoll, Michigan Department of Natural Resources, personal communication). Sharp's (1957:244) study in the Nebraska Sandhills indicated prairie-chickens decreased when pheasants increased, and when "pheasant(s) . . . crashed . . . prairie chickens then increased beyond all expectations . . . ." Declines of other species attributed to interactions with pheasants include black grouse (*Tetrao tetrix*) in the central European lowlands (Reichholf 1982), and Hungarian partridge (*Perdix perdix*) in Denmark (Westerskov 1964) and the United States (Kimmel 1988). The mechanisms that led to these declines are unknown, but suppressed hatchability of fertile host eggs in nests parasitized by pheasants may have been a key factor.

MANAGEMENT IMPLICATIONS

Our results support recommendations against introducing or managing to increase pheasants in areas supporting remnant flocks of prairie-chickens (Gross 1930, Cahalane et al. 1941, Grange 1948, Hamerstrom et al. 1957, Sharp 1957, Vance and Westemeier 1979). On Illinois sanctuaries, control of pheasants by habitat manipulations and opportunistic shooting (Westemeier 1988) during 1988–94 successfully eliminated parasitism of prairie-chicken nests. However, because prairie-chicken numbers did not increase thereafter, genetic and demographic enhancement may be necessary to maintain viable populations of prairie-chickens in Illinois (Westemeier et al. 1991, Westemeier and Jansen 1995, Bouzat et al. 1998). Until other limiting factors are better understood, we recommend limiting pheasant numbers on sanctuaries below levels observed during 1969–80. Further research is needed to determine if survival of young prairie-chickens with pheasants as brood mates is less than in normal broods. These efforts should be coupled with expanded management of grasslands as nesting and brooding habitat.

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